

RESEARCH ARTICLE

Biogeography of Stress: Graded and Threshold Phenological Responses in European Beech-Dominated Forests Under Disruptive Heatwaves

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Received: 30 September 2025 | **Revised:** 12 June 2026 | **Accepted:** 22 June 2026

Keywords: heat stress | legacy effect | MODIS EVI profiles | random forest | short-term impact

ABSTRACT

Climate change is increasing the frequency and intensity of summer heatwaves, posing a major threat to temperate forests. European beech (*Fagus sylvatica*) forests are particularly sensitive to thermal extremes. Given their wide distribution, responses to heatwaves are not uniform, and it remains unclear how sensitivity varies at the continental scale. This study aims to quantify how summer disruptive heatwaves (dHWs) reshape phenological dynamics in European beech-dominated forests (BDFs) over 2003–2023 across four major biogeographical regions: Alpine, Atlantic, Continental and Mediterranean. By combining remotely sensed vegetation time series with machine-learning and anomaly detection approaches, we specifically (i) identified the occurrence of summer dHWs across European BDFs; (ii) quantified the impacts of dHWs both on summer canopy functioning (short-term effect) and on autumn senescence phenology (lagged effect), and (iii) evaluated these phenological responses under different dHW intensity levels. Results revealed that dHWs in BDFs consistently reduced summer canopy greenness and advanced autumn senescence, with distinct regional patterns. The most pronounced dHW impacts were observed in Continental and Atlantic regions. Graded, intensity-dependent responses emerged in Atlantic, Continental and Alpine regions, with the latter showing a comparatively buffered response, likely due to a cooler climate baseline and shorter vegetative phase. By contrast, the Mediterranean region exhibited a threshold-type response, reflecting adaptation mechanisms of southern-edge populations under already limiting summer conditions. Late-summer and early-autumn emerged as the most sensitive time windows for dHW-induced phenological shifts, with temporal patterns varying along the European BDF climatic gradient. Together, these results demonstrate that dHWs drive both immediate and legacy impacts on forest vegetative dynamics, reducing seasonal productivity and advancing the end of the growing season, with intensity effects modulated by regional climate and baseline phenology. Our findings underscore the need for region-specific strategies to safeguard forest ecosystems as disruptive heatwaves continue to intensify.

1 | Introduction

Climate change is profoundly reshaping forest ecosystems, threatening their functioning and the essential services they provide, from carbon sequestration and water regulation to

biodiversity conservation (Psistaki et al. 2024). Alongside gradual warming, the most pressing risks stem from the increasing frequency and intensity of extreme climatic events, particularly heatwaves (HWs) (Hartmann et al. 2022). The occurrence of record-breaking high temperatures has increased

fivefold globally in recent decades (Coumou and Robinson 2013), and Europe has experienced most of its strongest HWs since the early 2000s (Khodayar Pardo and Paredes-Fortuny 2024; Lhotka and Kysely 2022). Defined as prolonged periods of anomalously high temperatures relative to local climatology (Perkins and Alexander 2013a), HWs are projected to intensify further in mid-latitude regions (Perkins-Kirkpatrick and Lewis 2020; Russo et al. 2015).

Heatwaves impose severe physiological stress on forests, impairing photosynthetic metabolism and stomatal conductance (Scafaro et al. 2021; Marchin et al. 2022), reducing canopy productivity (Ciais et al. 2005; Teskey et al. 2015), and in some cases triggering dieback and mortality events (Bauweraerts et al. 2014; Senf and Seidl 2021). Their impacts may extend beyond the event itself: HWs can cause direct leaf damage (Frei et al. 2022), reduce canopy leaf area (Filewod and Thomas 2013), and advance autumn senescence, thereby shortening the growing season and diminishing forest resilience in subsequent months (Frei et al. 2022; Kloos et al. 2024). Because leaf physiology is tightly coupled with seasonal dynamics, these disturbances are often expressed through productivity decline and shifts in phenology, which thus provide valuable indicators of ecosystem stress and recovery potential (Fu et al. 2020; Spafford et al. 2023).

In Europe, temperate deciduous forests, particularly those types dominated by beech (*Fagus sylvatica*) (Barbati et al. 2014), are regarded as highly vulnerable to thermal extremes (Rousi et al. 2022). However, tree responses are not uniform across the species' range, but are mediated by species-specific traits, local adaptation, and microclimatic buffering. Several studies have reported significant intra-species variability in phenotypic plasticity and tolerance thresholds across different climatic contexts (Benito Garzón et al. 2019; Fréjaville et al. 2019; Vitasse et al. 2009). Rita et al. (2020) and Margalef-Marrase et al. (2020) further demonstrated the strong spatial heterogeneity of forest responses to HWs: while some regions and forest types had clear NDVI decline, others showed little or no reduction, depending on baseline climate conditions, species composition, and topography. More recently, Zhou et al. (2025) and Wang et al. (2025) underlined the contribution of microclimatic conditions in buffering these responses, whereas Bonfanti et al. (2026) highlighted the role of leaf-out timing in modulating HW impact. Yet, when heatwaves have measurable impacts, it still remains unclear how biogeographical gradients—from cooler Alpine to hotter Mediterranean zones—shape forest phenological sensitivity to such disruption and the balance between graded responses, in which phenological shifts scale proportionally with HW intensity (Fu et al. 2022; Grossiord et al. 2020), and saturation-type responses, where stress reaches tipping points under extreme conditions (Arend et al. 2021; Li et al. 2023).

Remote sensing provides a powerful means of detecting HW-driven phenological disruptions at large scales. Vegetation indices such as the Enhanced Vegetation Index (EVI; Huete et al. 2002) capture canopy vitality, as well as its seasonal dynamics, and enable the identification of anomalies and stress responses across broad spatial and temporal domains (Decuyper et al. 2020; Gnilke and Sanders 2022). Ciais et al. (2005), via flux

towers, remote sensing, and modelling, showed that extreme summer heat caused a massive, measurable reduction in primary productivity across Europe, and that heatwaves suppress canopy carbon uptake and greenness during the stress event itself. Descals et al. (2023), to the contrary, detected and quantified a spatially widespread early leaf shedding (i.e., anomalously advanced senescence) across European deciduous forests, and linked it to preceding extremely high temperatures and aridity conditions. However, despite satellite data potential, continental-scale assessments remain limited in their ability to disentangle how phenological responses vary across biogeographical regions, from core to marginal populations, and under different HW intensity levels.

This study aims to fill this knowledge gap by combining satellite remote sensing with machine-learning and anomaly detection approaches to focus on effects of disruptive heatwaves (dHWs) on European beech-dominated forests (BDFs) across two decades and four major biogeographical regions. The main questions are: do disruptive heatwaves impact summer canopy dynamics and autumn senescence in European beech-dominated forests, and do the magnitude and timing of these phenological responses vary across biogeographical regions? These different levels of response represent a two-stage dHW impact pathway on phenology: an immediate disruption of canopy functioning and a lagged shift in phenological timing. The specific objectives therefore are to: (i) identify the occurrence of summer dHWs across European BDFs; (ii) quantify the short-term effects of dHWs on summer canopy activity and their lagged effects on autumn senescence timing across European BDFs across different biogeographical regions; and (iii) evaluate how such phenological responses vary across dHW intensity levels. By framing dHW impacts within a biogeographical perspective, our study provides novel insights into the resilience and vulnerability of Europe's dominant deciduous tree species under ongoing climate change.

2 | Materials and Method

2.1 | European Beech-Dominated Forest Data

The EU-Forest dataset of tree occurrences published by Mauri et al. (2017; <https://doi.org/10.6084/m9.figshare.c.3288407>) was used as a reference for identifying the beech forest locations across Europe. This 1-km gridded dataset provides a detailed and harmonized description of European tree species distribution, integrating data from Forest Focus and Biosoil databases and from National Forest Inventories.

Consistent with previous studies (Bajocco et al. 2019, 2025; Cesaretti et al. 2025; Ferrara et al. 2023), to approximate dense and spatially continuous BDF areas, three spatial filters were applied. First, only EU-Forest beech cells with centroids located within the distribution range of European beech provided by the EUFORGEN Programme (<https://www.euforgen.org>) were retained. Second, we used the European Forest Types (EFT) gridded dataset (<https://doi.org/10.5281/zenodo.18496150>), developed within the Horizon Europe OptFor-EU project, as reference map for beech dominance. This product provides a 100 m-resolution pan-European classification of

forest types following a rule-based expert system (Giannetti et al. 2026), and beech forest (category 6) and mountainous beech forest (category 7) types were used to filter the EU-Forest cell centroids. Third, we intersected the resulting cell centroids with the 2018 CORINE Land Cover (CLC) map (<https://land.copernicus.eu/en/products/corine-land-cover>), using the broad-leaved forest class (CLC 311) to exclude isolated, fragmented, or non-forest beech presences and to ensure that cell centroids fell in spatially coherent forested landscapes. We considered the dataset resulting from this three-level filtering as representative of beech-dominated forest conditions in a continental-scale analysis.

Finally, to account for the ecological and climatic variability across the range of European BDFs, the classification of biogeographical regions was adopted (Roekaerts 2002). Four main regions were considered for the analysis: Alpine, Atlantic, Continental and Mediterranean. The final database consisted of 8546 observations in total (Figure 1). delineate study areas and do not necessarily depict accepted national boundaries.

2.2 | Heatwave Detection

A HW is defined as a prolonged period of unusually high temperatures compared to the average climatic conditions for a given area and time of year (Perkins 2015). However, no universally agreed benchmark for HW temperature and duration exists, as conditions vary across geographical regions and climatic contexts (Awasthi et al. 2022). In this study, for Europe, we considered a HW as a period of at least three consecutive days during which the daily maximum temperature exceeds the corresponding calendar-day 90th percentile, based on a 30-year climatological reference period (Perkins and Alexander 2013; Russo et al. 2015).

Temperature data (Tmax and Tmin) were obtained from ERA5-Land Daily Aggregated (ECMWF Climate Reanalysis), which provides daily data at a 9km spatial resolution. For each year within the analysis period (2003–2023), the reference climatology was computed using data from the previous 30-year window, requiring temperature data from 1972 to 2023 (e.g., 1972–2002 climatology for the 2003 target year). This shifting climatology approach was adopted to limit the influence of warming trends during the last

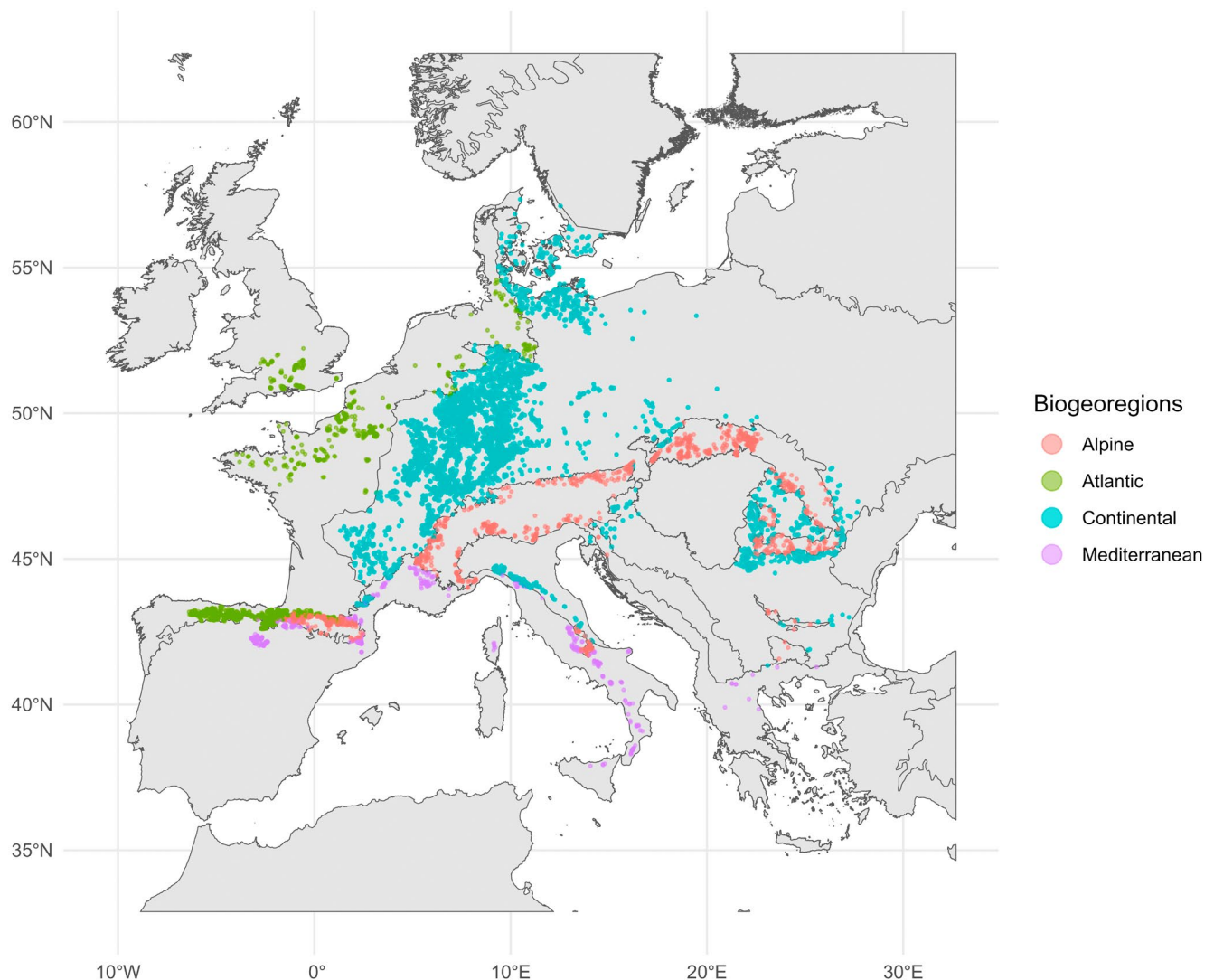


FIGURE 1 | European beech-dominated forest locations across biogeographical regions. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

decades on HW detection, as reported in many previous studies (Giménez et al. 2024; Rosselló et al. 2023; Wang et al. 2022).

As a first step, a threshold was defined individually for each observation, based on daily $T_{\max}$ and $T_{\min}$ values within the baseline period. The baseline comprises a 30-year reference window used to compute the seasonally varying climatology and the upper threshold applied for HW detection (Hobday et al. 2016). Climatology was calculated by grouping temperature data by day-of-year (DOY) and applying a two-step rolling-mean smoothing to minimize day-to-day fluctuations and keep only seasonal signals (Hobday et al. 2016). According to Hobday et al. (2016), a 5-day double-sided window (11-day total width) was applied, followed by a second smoothing pass with a 15-day double-sided window (31-day total width). The upper threshold was defined as the 90th percentile of $T_{\max}$ time series, while the lower threshold was based on the average $T_{\min}$ and $T_{\max}$ data over the baseline (Hobday et al. 2018). HW events were then categorized into two intensity levels (Hobday et al. 2018): (i) moderate intensity when the maximum intensity did not double the distance between the seasonal climatology and the threshold; (ii) strong intensity when the maximum intensity doubled or exceeded this distance. For this study, only HWs occurring during the summer months (i.e., from the beginning of June to the end of September) were considered. HW detection was carried out using the HeatwaveR package (Schlegel and Smit 2018).

2.3 | Phenological Anomaly Detection

The combination between MODIS (Moderate Resolution Imaging Spectroradiometer) MOD13Q1 and MYD13Q1 Enhanced Vegetation Index (EVI) products (250m spatial resolution and 8-day temporal frequency) was used to extract European BDF seasonal profiles for the period 2003–2023 (Didan 2021a, 2021b). Considering only MODIS pixels covering the three-level filtered grid cell centroids allowed minimizing the risk of losing valid BDF pixels due to the mismatch between 250m MODIS pixel and 1km EU-Forest grid, while retaining the finer-scale variability.

To detect phenological anomalies (PAs) directly induced by summer heatwaves, the analysis was limited to the period from the beginning of June (DOY 153) to the end of September (DOY 273). For each site and year, EVI values falling outside the 90% threshold of the probabilistic distribution were classified as anomalous.

Phenological anomalies were detected using the *npphen* R package (Estay and Chávez 2018). It applies a two-dimensional kernel density estimation (KDE) to account for annual vegetation phenological behavior and its variability (Figure 2). The advantage of this approach is its flexibility in adapting to site-specific conditions and accounting for natural interannual variability (Decuyper et al. 2022). The algorithm operates on the entire dataset without requiring pre-processing steps such as outlier removal (Fuentes et al. 2024). The result is a probabilistic estimate of the expected annual phenology based on the observed data (Chávez et al. 2023). Anomalies are then identified as values falling outside a given threshold of the probabilistic distribution (Decuyper et al. 2022).

Among observations experiencing HWs, those exposed to HWs but showing no PA were classified as “resilient.” In contrast, observations exhibiting at least 1 year with a PA, in which the HW event preceded the observed PA, were classified as “affected”, and the corresponding HW event was considered disruptive (i.e., dHWs). Observations with no HW and no PA were classified as “unaffected” and were used as control in the following analysis.

2.4 | Heatwave Impact Analysis

To assess the short-term canopy response to HWs, we computed the summer EVI integral (SI), which reflects cumulative canopy greenness over the summer period, from the start of June (DOY 153) to the end of September (DOY 273), in each biogeographic region and for resilient, affected and unaffected observations. SI is a phenology metric of seasonal canopy activity and vegetation condition, and its decline reflects impaired photosynthetic activity and/or significant leaf damage during the stress period. The summer integral was computed as the area under the curves using a natural spline interpolation, with the *MESS* R package (Ekström 2012). Then, to assess the lagged impact of HWs, we computed the senescence date (SD) of resilient, affected, and unaffected beech-dominated forests. SD is a metric directly measuring phenological timing, and its advancement represents a shift in the timing of a discrete seasonal transition (onset of autumn senescence) as a consequence of prior heat stress. First, we linearly interpolated the EVI profiles; then, we identified the senescence date as the day of year (DOY) when the declining curve crossed the 50% threshold, computed as follows (Zeng et al. 2020):

$$EVI_{\text{threshold}} = EVI_{\text{base}} + 0.5 \times (EVI_{\text{max}} - EVI_{\text{base}}) \quad (1)$$

where EVI_{max} is the seasonal maximum of the fitted EVI curve, representing peak canopy greenness, and EVI_{base} is the baseline EVI, typically the minimum value of the curve outside the growing season (late winter in our case).

Since “resilient” is conceptually not an impact class, but rather a non-damaged response (maintenance of function) or a recovery/avoidance class, we focused only on “affected” BDF profiles, that is, from disruptive heatwaves with detectable impacts. To confirm that affected and resilient observations represent functionally distinct responses to HWs, for each biogeographic region, we fitted linear mixed-effects models (LMMs) (Nakagawa and Schielzeth 2012; Oberg and Mahoney 2007), using SI and SD as response variables and “unaffected” as baseline, with site and year included as random effects. To perform the LMMs, we used the *lme4* R package (Bates et al. 2015).

Then, to investigate whether disruptive heatwave intensity-response relationships vary across biogeographical regions and to characterize their patterns, we fitted generalized additive mixed models (GAMMs) in which standardized dHW intensity was included as a smooth term ($k=5$), allowing for potential non-linear responses while retaining the random-effects structure used in the previous LMM analysis. To perform the GAMMs, we used the *gam4* R package (Wood 2025).

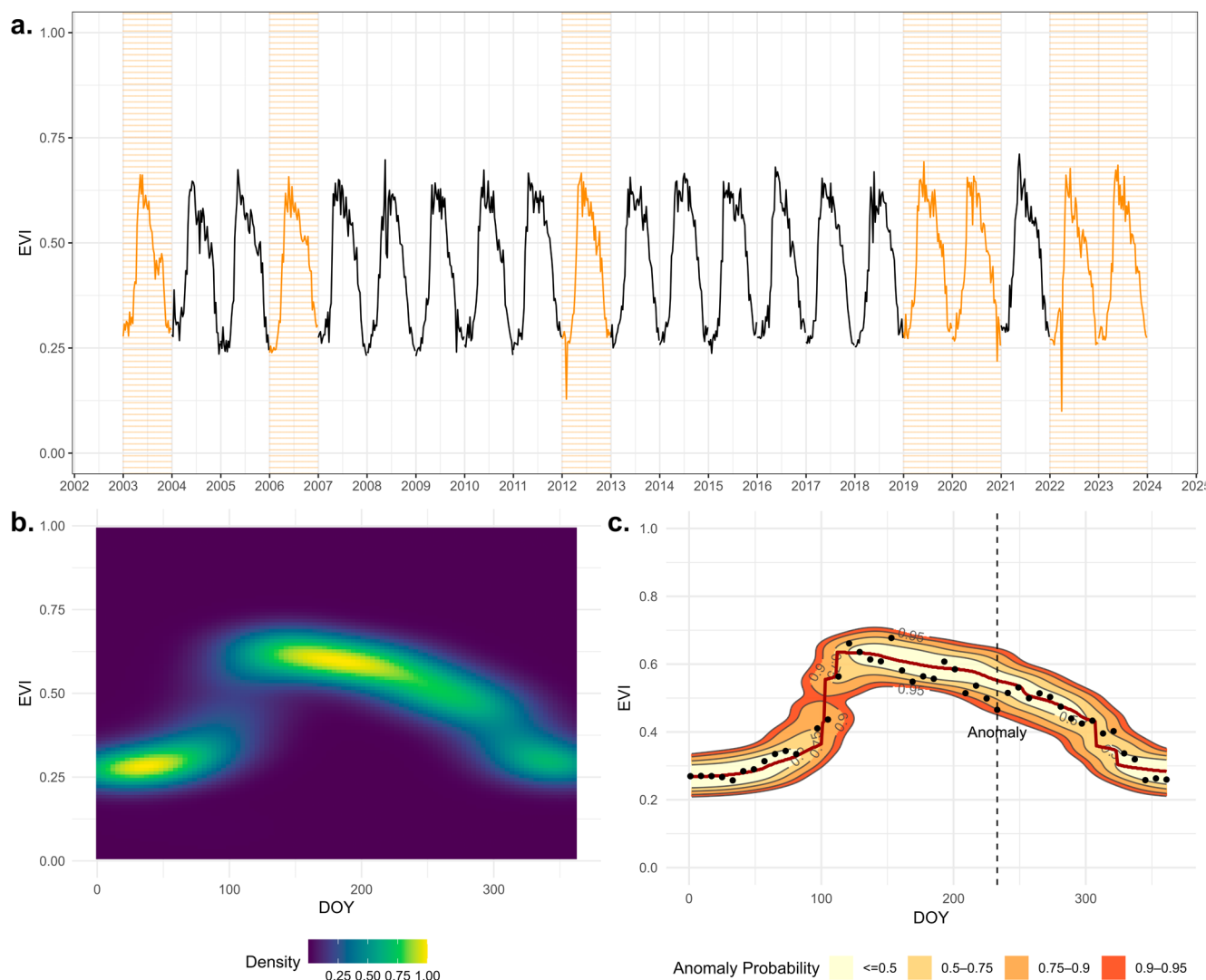


FIGURE 2 | Anomaly detection in EVI temporal profiles. (a) Example of a complete EVI time series from a beech-dominated forest site; years experiencing HW are highlighted in orange. (b) Two-dimensional KDE based on all annual observations for the year 2022, shown as an example. (c) Phenological baseline (red line) and anomaly probability (isolines with thresholds values) for the year 2022, shown as an example; EVI observations (black dots) include one anomalous point outside the 90% probability distribution, indicated by the vertical dashed line.

Given the non-linearity of the responses, the impacts of dHWs across biogeographical regions were further examined by intensity level. Differences in SI and SD between unaffected profiles and those moderately and strongly affected were assessed using the non-parametric Wilcoxon test, with statistical significance set at $p = 0.05$.

Finally, to identify the seasonal periods most impacted by dHWs during the greendown and senescence phases, a Random Forest (RF) analysis (Breiman 2001) was performed using the EVI temporal bands spanning summer and autumn phenology, that is, from early June (DOY 153) to late November (DOY 329). The analysis was performed using the randomForest and caret R packages (Kuhn 2008). The RF classifier was trained separately for each biogeographical region, for both moderate and strong dHWs (number of trees = 500) in affected observations. Variable importance was assessed through mean decrease in accuracy (Han et al. 2016).

For the sake of consistency, the whole methodological flow was also repeated for resilient observations (see [Supporting Information](#)).

3 | Results

3.1 | Heatwave Regional Characterization

Across the four biogeographical regions, a total of 83,488 HW events were recorded during 2003–2023. Approximately 27% of them were associated with the occurrence of phenological anomalies, resulting in 22,567 disruptive heatwaves. The other 60,921 events (73%) were associated with non-disruptive HW events. In total, the Continental region accounted for the highest number of dHWs, with 63% of events, followed by the Atlantic (21%), Alpine (11%), and Mediterranean (5%) regions.

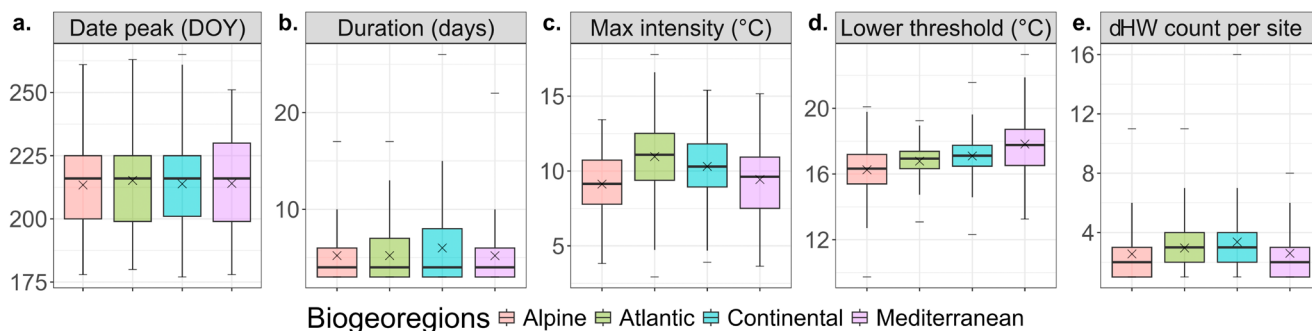


FIGURE 3 | Summary statistics of dHWs detected across the four biogeographical regions: (a) peak date, that is, the day of the year (DOY) corresponding to the maximum dHW intensity, (b) dHW duration, (c) maximum intensity above climatological baseline, (d) lower temperature threshold, that is, site-specific average temperature across the climatological baseline, (e) average number of dHW events per site. Boxes represent the interquartile range (i.e., the 1st and 3rd quartiles), and whiskers extend to 1.5 times the interquartile range. The horizontal line and the cross symbol within each box indicate the median and the mean, respectively. Outliers are shown as individual dashes.

According to the dHW main statistics (Figure 3), no substantial differences were observed in the peak date (expressed as day of year, DOY) across biogeographical regions: mean values ranged from DOY 213 to DOY 215 (early August), with a standard deviation ($\pm$ SD) between 16 and 18 days. Similarly, the average dHW duration was consistent across regions, generally ranging around 5 days ($\pm$ 3 days), except in the Continental region, which showed slightly longer durations (6 ± 4 days). This pattern is also reflected in the distribution, where the Continental region showed higher dispersion in the interquartile range, indicating generally longer events. Notably, a few sites in the Continental and Mediterranean regions experienced exceptionally long dHWs, with durations reaching up to 26 days in 2018 and 22 days in 2003, respectively. In terms of maximum intensity, the Atlantic and Continental regions displayed the highest values, with mean peaks exceeding 10°C ($\pm 2^{\circ}\text{C}$) above the climatological baseline. As expected, the lower temperature threshold, defined as the site-specific average temperature over the years, reflected the general temperature gradient across Europe, with higher values in the Mediterranean and lower in the Alpine region. Finally, the average number of dHW events per site was similar across the regions, around $3 (\pm 2)$ events per site. However, maximum site-level dHW frequencies varied among regions, reaching up to 16 events in the Continental region, 11 in both the Alpine and Atlantic regions, and 8 in the Mediterranean region during the study period. The relative frequency of moderate and strong dHWs varied substantially across biogeographical regions. In the Alpine region, moderate events dominated (71%), with strong dHWs accounting for only 29%. The Continental region displayed a similar but less accentuated pattern, with 59% moderate and 41% strong events, followed by the Mediterranean region, with 53% moderate and 47% strong events. In contrast, the Atlantic region exhibited an opposite pattern, with 46% and 54% for moderate and strong events, respectively.

3.2 | Disruptive Heatwaves' Impact Assessment

Region-specific linear mixed-effects models showed consistent differences between resilient and affected observations relative to the unaffected condition for both summer and autumn BDF phenology (Figure 4). Across all regions, the dHW-affected observations exhibited a significantly lower summer EVI integral

(SI) and an advance of senescence date (SD) compared with unaffected observations, indicating reduced cumulative summer canopy activity and earlier seasonal shutdown under impacted conditions (Alpine: SI -0.59 , SD -3.85 ; Atlantic: SI -0.76 , SD -3.55 ; Continental: SI -1.86 , SD -9.24 ; Mediterranean: SI -0.23 , SD -5.70 ; all $p \leq 0.01$). On the opposite, the resilient observations showed a contrasting pattern: SI was higher than unaffected in Alpine ($+0.09$) and Mediterranean ($+0.20$), lower in Continental (-0.47), and not different in Atlantic (ns), while SD was generally earlier than unaffected in Alpine (-1.32), Continental (-2.69) and Mediterranean (-2.08), but not in Atlantic (ns). These patterns highlight a robust negative shift in both summer productivity and senescence timing in affected BDF observations. To the contrary, resilient showed small and/or non-significant effects relative to the unaffected (notably in the Atlantic, and partially for SI elsewhere), ranging from maintained or even enhanced summer activity to only partial phenological buffering (see [Supporting Information](#)).

Fitting the GAMMs for affected observations revealed marked regional differences in how the summer EVI integral responds to standardized maximum dHW intensity (Figure 5). In the Mediterranean region, the smooth term was highly significant and clearly non-linear (effective degrees of freedom, $\text{edf} = 3.588$, $p < 0.0001$), with SI remaining relatively stable under low-to-moderate intensities but then declining sharply as intensity increased, followed by a plateau at the highest intensities where further increases in dHW intensity produced comparatively little additional reduction in SI. The Continental region showed the strongest response overall ($\text{edf} = 3.764$, $p < 0.0001$), characterized by a pronounced non-linear decrease in SI with increasing intensity, steeper in moderate and slowing at stronger values, consistent with the high sensitivity of summer canopy activity to disruptive heatwave intensity. The Atlantic region also exhibited a significant non-linear relationship ($\text{edf} = 3.723$, $p < 0.0001$), but with a weaker and more complex shape, suggesting partial buffering at intermediate intensities and a stronger decline occurring only at the upper tail of intensity. In contrast, the Alpine region showed no evidence of a relationship between dHW intensity and SI ($\text{edf} = 1$, $p = 0.38$), either indicating that alpine systems are less impacted in SI by intensity (possible buffering due to temperature limitation and/or differences in phenology), or that narrower and noisier intensity range masks any underlying relationship.

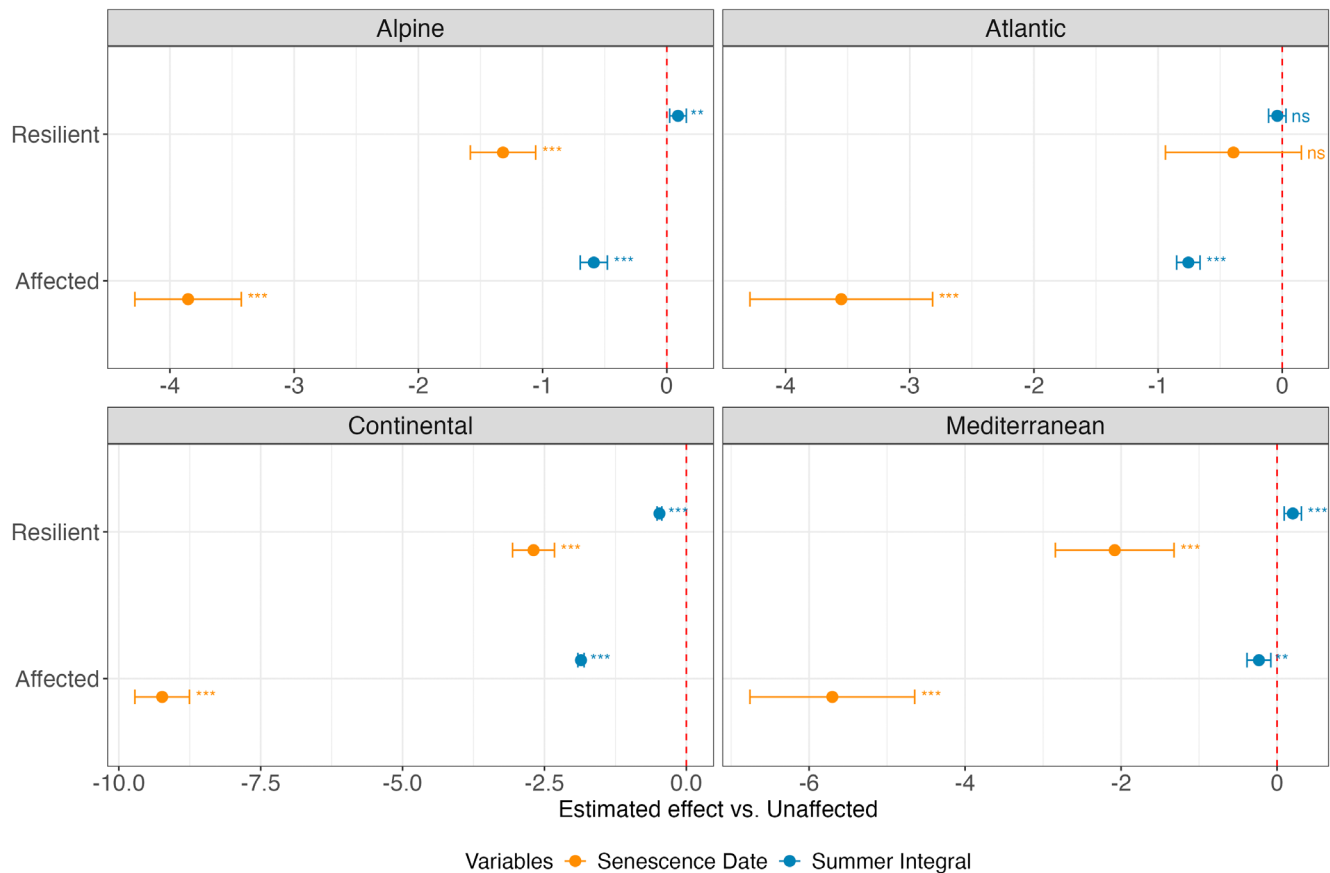


FIGURE 4 | Forest plot of region-specific linear mixed-effects model estimates quantifying differences in summer EVI integral (blue) and senescence date (orange) for affected and resilient observations relative to the unaffected category across Alpine, Atlantic, Continental, and Mediterranean regions. Points represent fixed-effect coefficients (estimated effect vs. unaffected), horizontal bars indicate 95% confidence intervals, and the red dashed line marks zero (no difference from unaffected). Significance codes are shown next to each estimate (*** $p < 0.001$; ** $p < 0.01$; ns = not significant). Models were fitted separately by region with random intercepts for site and year.

In line with SI, region-specific GAMMs indicated that dHW intensity significantly shaped also the senescence date in all biogeographical regions, but with contrasting functional forms (Figure 5). In the Mediterranean region, the relationship was strongly non-linear ($\text{edf} = 3.572$, $p < 0.0001$): SD decreased progressively with increasing disruptive heatwave intensity, with a marked drop around average-to-moderately high intensity values, followed by an evident saturation at the upper end of the intensity gradient, suggesting that beyond a certain severity further increases in dHW intensity advance senescence only marginally. The Alpine region showed a robust, essentially linear advancement of senescence with increasing intensity ($\text{edf} = 1$, $p < 0.0001$). In contrast, Atlantic and Continental regions exhibited significant but more complex non-linear responses ($\text{edf} = 3.781$ and $\text{edf} = 3.824$, respectively; $p < 0.0001$), indicating that SD progressively advances, but the magnitude of SD shifts depends on the intensity range considered, and was more pronounced in Atlantic than in Continental. Overall, the Mediterranean saturation behavior is consistent with a threshold-type response of late-season canopy dynamics to extreme heat stress, pointing to diminishing marginal impacts of additional intensity once strong disruptive heatwaves occur.

The observed non-linearities support the use of intensity classes (e.g., moderate vs. strong dHWs) rather than assuming a strictly

linear response gradient, thereby providing a categorical framework for comparing BDF functioning under distinct levels of disruptive heatwave intensity.

The average affected EVI profiles showed a clear inflection from the beginning of June to the end of September compared to the unaffected ones, across all biogeographical regions (Figure 6). The magnitude of this inflection was positively related to intensity levels, with strong dHWs inducing larger declines in EVI than moderate ones, with drops mainly occurring after the seasonal peak (DOY ~200). In the Alpine region, differences between unaffected and affected profiles were relatively modest and mainly occurred at the beginning and at the end of the summer season. The Continental and Atlantic regions showed more pronounced reductions, particularly during late summer and early autumn, where strong dHWs led to a visibly lower EVI compared to unaffected conditions. By contrast, in the Mediterranean region, while moderate dHWs already caused a marked reduction in EVI, the additional impact of strong dHWs was limited, so that the gap between moderate and strong categories remains small. Overall, the profiles indicate that dHWs primarily accelerate canopy decline in late summer to autumn in Alpine, Continental, and Atlantic regions, while in the Mediterranean region BDFs exhibit a generally depressed greenness trajectory irrespective of dHW intensity.

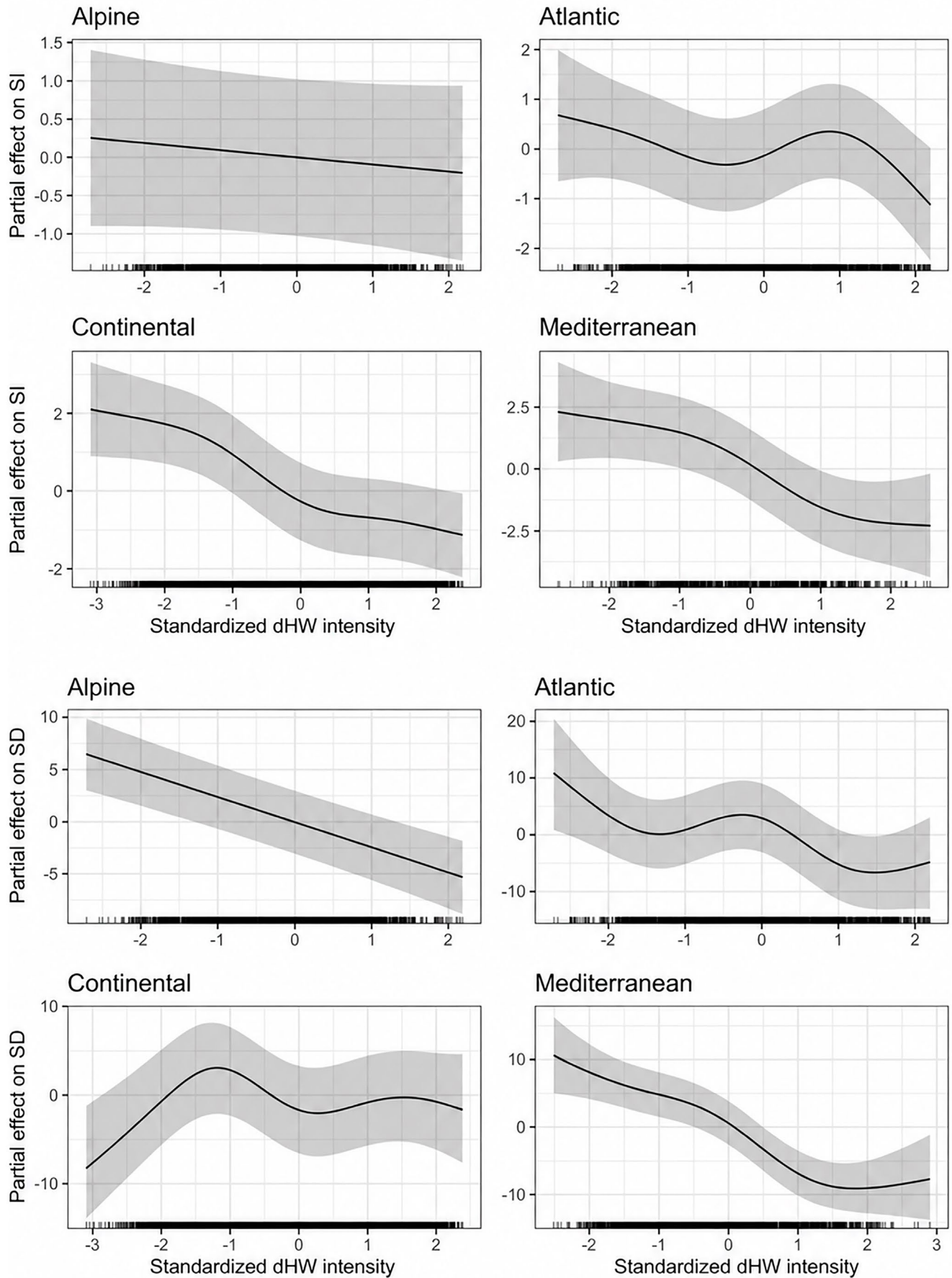


FIGURE 5 | Legend on next page.

FIGURE 5 | Region-specific generalized additive mixed-model (GAMM) smooths in affected BDF observations, describing the relationship of standardized dHW intensity with summer integral (SI) and senescence date (SD) across Alpine, Atlantic, Continental, and Mediterranean regions. Black lines show the estimated smooth partial effect of dHW intensity on the dependent variables (SI and SD), with grey shading indicating the 95% confidence interval. Rug marks along the x-axis denote the distribution of observations.

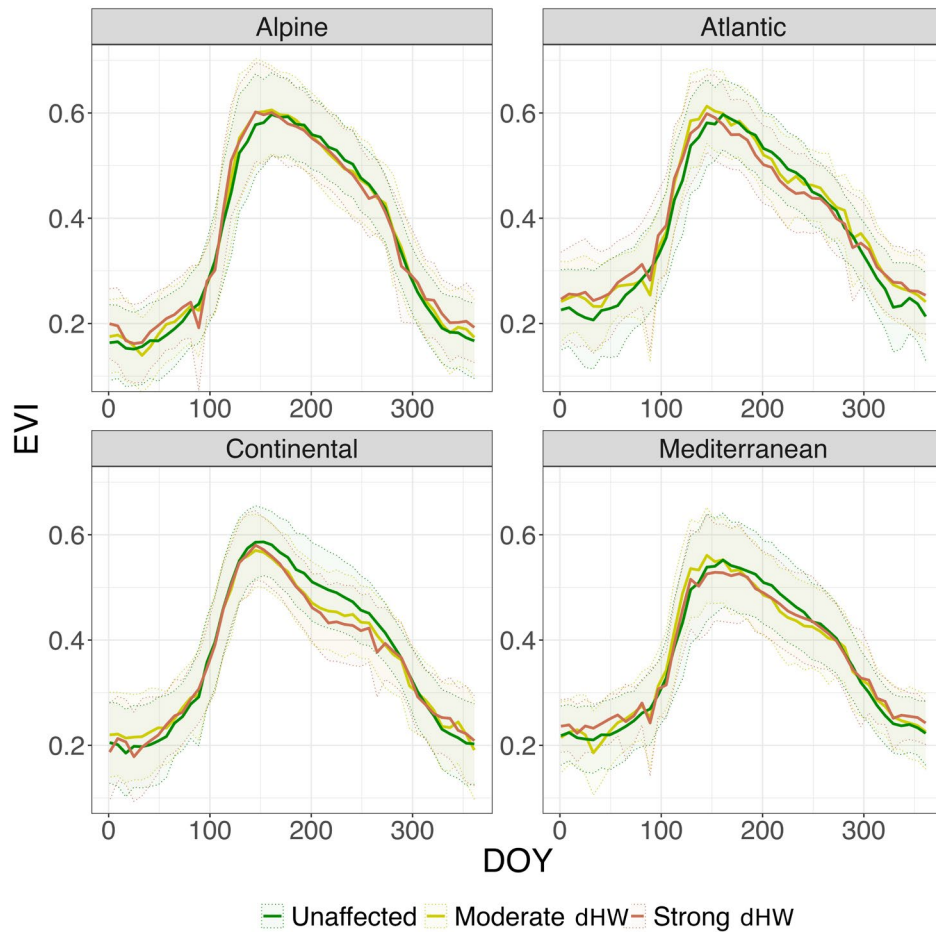


FIGURE 6 | Affected average EVI temporal profiles across biogeographical regions and their standard deviation (shaded areas). Unaffected refers to EVI profiles of BDF observations that have not experienced either HWs or PAs, while “Moderate” and “Strong” indicate the corresponding intensity level of heatwaves in affected profiles that have experienced both HWs and PAs.

The SI analysis reveals a gradual decrease across all biogeographical regions when comparing unaffected profiles to those associated with moderate and strong dHW events (Figure 7). In the Continental region, the mean integral value decreased by around 6% under moderate dHWs and 8% under strong dHWs. A similar trend was observed in the Atlantic region, with mean SI decreasing by approximately 1% and 5% under moderate and strong dHWs, respectively. The Alpine region showed a less pronounced decline compared to the previous regions: about 1% for moderate dHWs and 2% for strong dHWs. In the Mediterranean region, the difference between intensity categories was the least marked, with mean SI decreasing by approximately 3.5% for both moderate and strong dHWs.

The analysis of SD in autumn phenology revealed a gradual advance of leaf senescence in BDFs affected by dHWs across all biogeographical regions (Figure 7). Compared to unaffected

profiles, those exposed to moderate and strong dHWs showed earlier senescence dates, with the magnitude of the shift generally increasing with dHW intensity. In the Continental region, senescence occurred approximately 8 days earlier under moderate dHWs and 10 days earlier under strong dHWs. A similar pattern was observed in the Atlantic region, where the shift reached up to 4 days under moderate dHWs and up to 13 days under strong dHWs. The Alpine region showed a more buffered response, with senescence occurring 3 and 6 days earlier under moderate and strong dHWs, respectively. In contrast, the Mediterranean region presented a less consistent pattern, with moderate dHWs advancing senescence by 6 days, while strong dHWs advanced it by 4 days, suggesting a potential saturation effect under extreme conditions.

Statistical analysis confirmed that the differences in SI are significant across all dHW categories in the Atlantic ($p < 0.0001$)

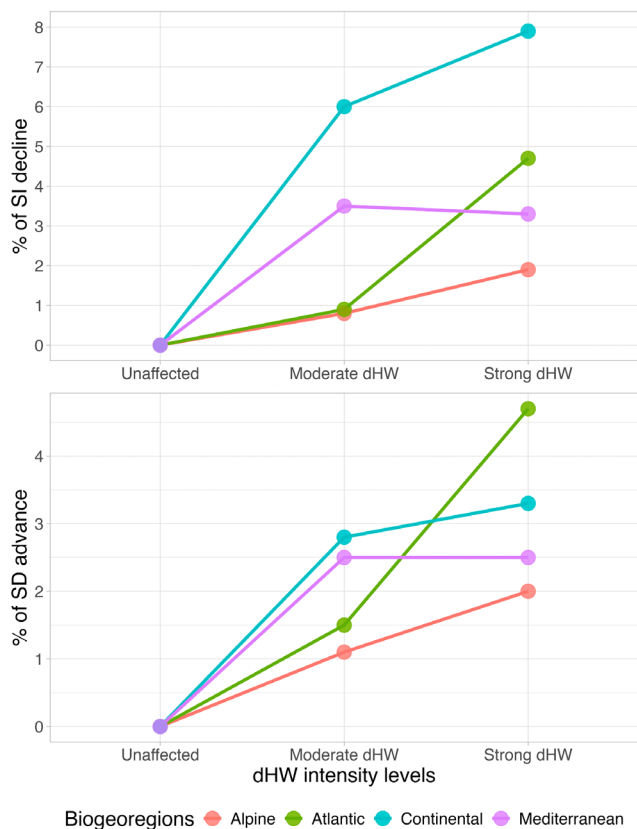


FIGURE 7 | Percentage of mean summer EVI integral (SI) decline (top) and senescence date (SD) advance (bottom) according to dHW occurrence and intensity in affected observations, across the four biogeographical regions.

and Continental ($p < 0.0001$) regions (Figure 8). The Alpine region, though exhibiting significant differences with the unaffected observations for both moderate and strong dHWs ($p < 0.01$ and $p < 0.0001$, respectively), showed similar behavior between the intensity levels. This finding clearly demonstrates that dHWs have a significant negative impact on the seasonal productivity of BDFs and that there is a consistent dose–response relationship: as the intensity of the dHW increases from moderate to strong, the overall seasonal greenness decreases, yet the magnitude and sensitivity of the responses vary among regions. The stronger decline observed in the Atlantic and Continental regions highlights their higher vulnerability to dHWs, while the Alpine region shows comparatively buffered responses, possibly due to cooler baseline conditions and a delayed growing season, which together mitigate the exposure to peak summer heat stress. In contrast, the Mediterranean region revealed significant differences between affected and unaffected profiles ($p < 0.0001$), but no significant difference between the affected profiles ($p > 0.5$). This pattern in the Mediterranean region confirms a threshold-type response rather than a graded sensitivity, likely driven by a possible saturation effect under intensifying summer heat stress.

Statistical analysis of SD confirmed significant shifts in senescence for all dHW intensity levels in Alpine ($p < 0.001$) and Continental ($p < 0.01$) regions (Figure 8). In the Atlantic region, only the comparison between unaffected and moderate dHW was not significant ($p = 0.5$), suggesting a threshold-type effect

in the advance of leaf senescence. In the Mediterranean region, senescence occurred significantly earlier under moderate dHWs compared to unaffected profiles ($p < 0.001$), but no further significant shift was observed under strong dHWs, indicating a saturation effect under already warm baseline conditions. Overall, the comparisons confirm a progressive advancement of senescence with increasing dHW severity. However, while dHWs consistently accelerate leaf senescence, the magnitude and progression of this response are modulated by regional climatic conditions.

The RF analysis identified which time periods within the summer and autumn months were most informative for dHW-induced PAs, revealing temporally distinct patterns across the biogeographical regions and among the dHW intensity categories (Figure 9). The results consistently highlighted, for both moderate and strong dHWs, two distinct periods where the impact of the disruptive heatwave was most pronounced: late summer (mid-August to early-September) and autumn (late-September to late-October). While the two-peak pattern is common, its timing and intensity vary by climatic region, revealing different regional responses to the dHWs. In the Alpine zone, moderate impacts were expressed through a two-peak pattern, but strong dHWs were dominated by an overwhelming late-summer impact on canopy greenness. In Continental forests, moderate impacts showed both summer and autumn signals, while strong impacts amplified both phases, with particularly high importance scores in late September. Atlantic forests revealed a dominant autumn signal across both moderate and strong impacts, but the latter drastically intensified the October peak. In Mediterranean sites, moderate impacts were best distinguished during the summer peak, while strong impacts shifted the dominant signal toward autumn, reflecting a powerful legacy effect on senescence. Notably, unlike moderate dHWs, strong dHWs revealed a clear temporal gradient in the most important bands, aligned with the biogeographical thermal gradient, from earlier bands in the cooler Alpine region to later bands in the warmer Mediterranean region. Overall, the analysis demonstrates that increasing dHW severity not only amplifies the detectability of phenological disruption but also alters the temporal windows where damage is most pronounced.

4 | Discussion

By integrating remotely sensed EVI temporal profiles, anomaly detection, and machine learning approaches, this study provides continental-scale evidence that summer disruptive heatwaves (dHWs) represent a significant driver of phenological shift in European beech-dominated forests (BDFs), with effects that vary across biogeographical regions. Our analyses distinguish two sequential levels of impact: a short-term disruption of summer canopy activity, captured by the seasonal EVI integral (SI), which reflects canopy greenness and photosynthetic performance during the stress period; and a lagged phenological response, measured by the senescence date (SD), which directly captures shifts in the timing of autumn leaf senescence as a downstream consequence of prior thermal stress.

There may be HW events that, even if strong, do not impact forest phenology, likely because local environmental conditions

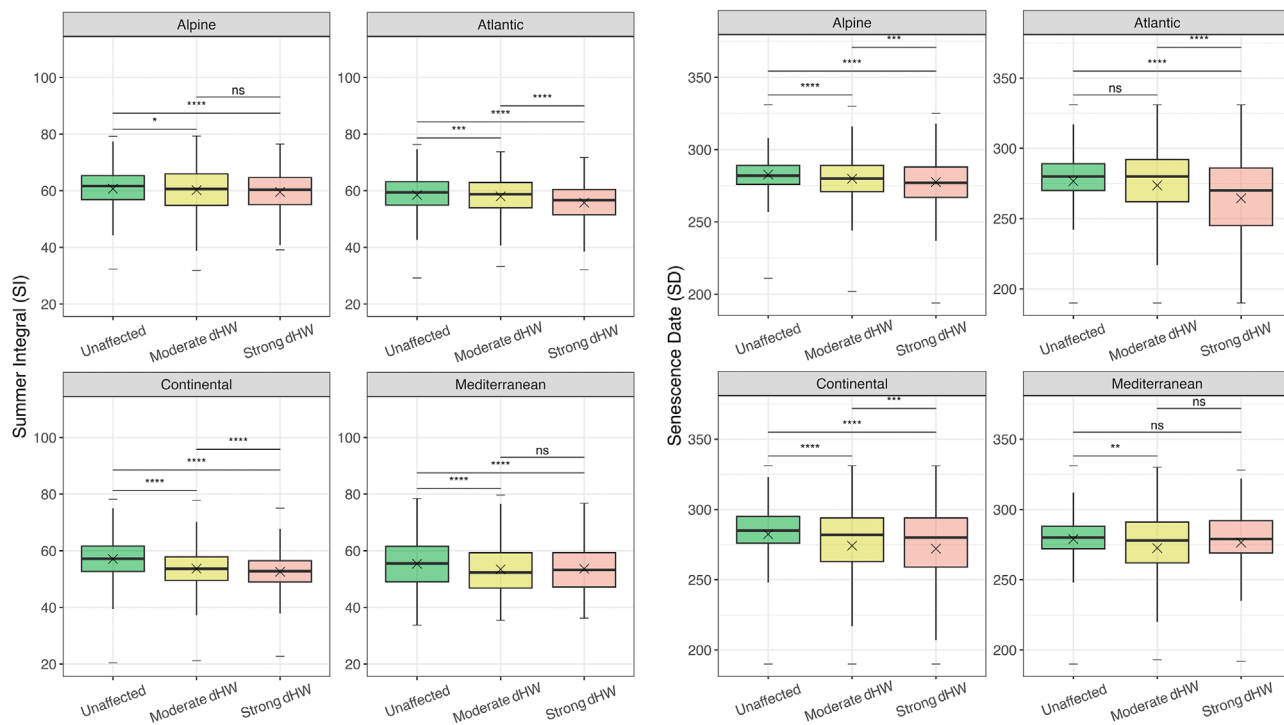


FIGURE 8 | Summer integral (SI) and senescence date (SD) distribution across biogeographical regions for unaffected (green boxes) and affected profiles (yellow boxes for moderate, red boxes for strong). Significant differences between categories are reported as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$, ns = non-significant. Boxes represent the interquartile range (i.e., the 1st and 3rd quartiles), and whiskers extend to 1.5 times the interquartile range. The horizontal line and the cross symbol inside each box represent the median and the mean, respectively. Outliers are shown with an individual dash.

dampen damage and allow forests to buffer the weather anomaly (Rita et al. 2020; Margalef-Marrase et al. 2020; Wang et al. 2025; Bonfanti et al. 2026). In our study, affected and resilient observations showed distinct response patterns, indicating that the two categories capture different ecological states. Accordingly, the resilient observations can be interpreted as a largely non-damaged, low-to-not impacted category that is closer to unaffected than to affected. Since our objective was to quantify disruptive heatwave impacts (i.e., negative deviations in seasonal activity and/or advanced senescence), we focused only on affected observations; resilient observations, by definition showing limited functional/phenological disruption, were not used to estimate the magnitude and timing of negative impact.

Results revealed three key insights on dHWs: (i) they consistently reduce canopy greenness during summer, with intensity-dependent differences in most regions, but saturation-type responses in Mediterranean sites; (ii) they advance autumn senescence across the species range, with the strongest shifts in Continental and Atlantic forests; and (iii) the timing and magnitude of these responses vary systematically along Europe's climatic/altitudinal gradient.

4.1 | Short-Term Impact of Disruptive Heatwaves

Across all regions, dHWs reduced BDF summer canopy greenness, confirming previous studies on impaired physiology

under thermal extremes (Ciais et al. 2005; Teskey et al. 2015; Xu et al. 2020), with direct implications for carbon sequestration and overall ecosystem health (Bastos et al. 2014; Moore et al. 2021). The integral analysis supports a dose-response relationship in Alpine, Atlantic, and Continental regions, where stronger dHWs produced proportionally greater reductions in greenness.

The Continental and Atlantic regions emerged as the most vulnerable, exhibiting the greatest proportional decrease in EVI integrals, especially under strong dHWs. This heightened sensitivity can be attributed to several factors. Firstly, these regions experienced dHWs with the highest maximum intensity (exceeding +10°C above baseline). The finding that the Continental region experienced the highest number of dHWs, while the Atlantic region had the highest proportion of strong dHWs, is critical and suggests that beech-dominated forests in these regions are particularly exposed to heat stress compared to the others. Secondly, BDFs in these areas often grow under mesic conditions near their physiological optimum; while productive, they may have evolved fewer defensive mechanisms against frequent and intense heat stress compared to marginal populations, making them more vulnerable to sudden thermal stress (Baumbach et al. 2019; Cavin and Jump 2017; Leuschner 2020; Muffler et al. 2020). At the physiological level, heightened vulnerability in mesic regions reflects the stomatal behavior of European beech (Zeppan et al. 2026): mature trees maintain open stomata and high transpiration rates even under moderate water deficit, sustaining

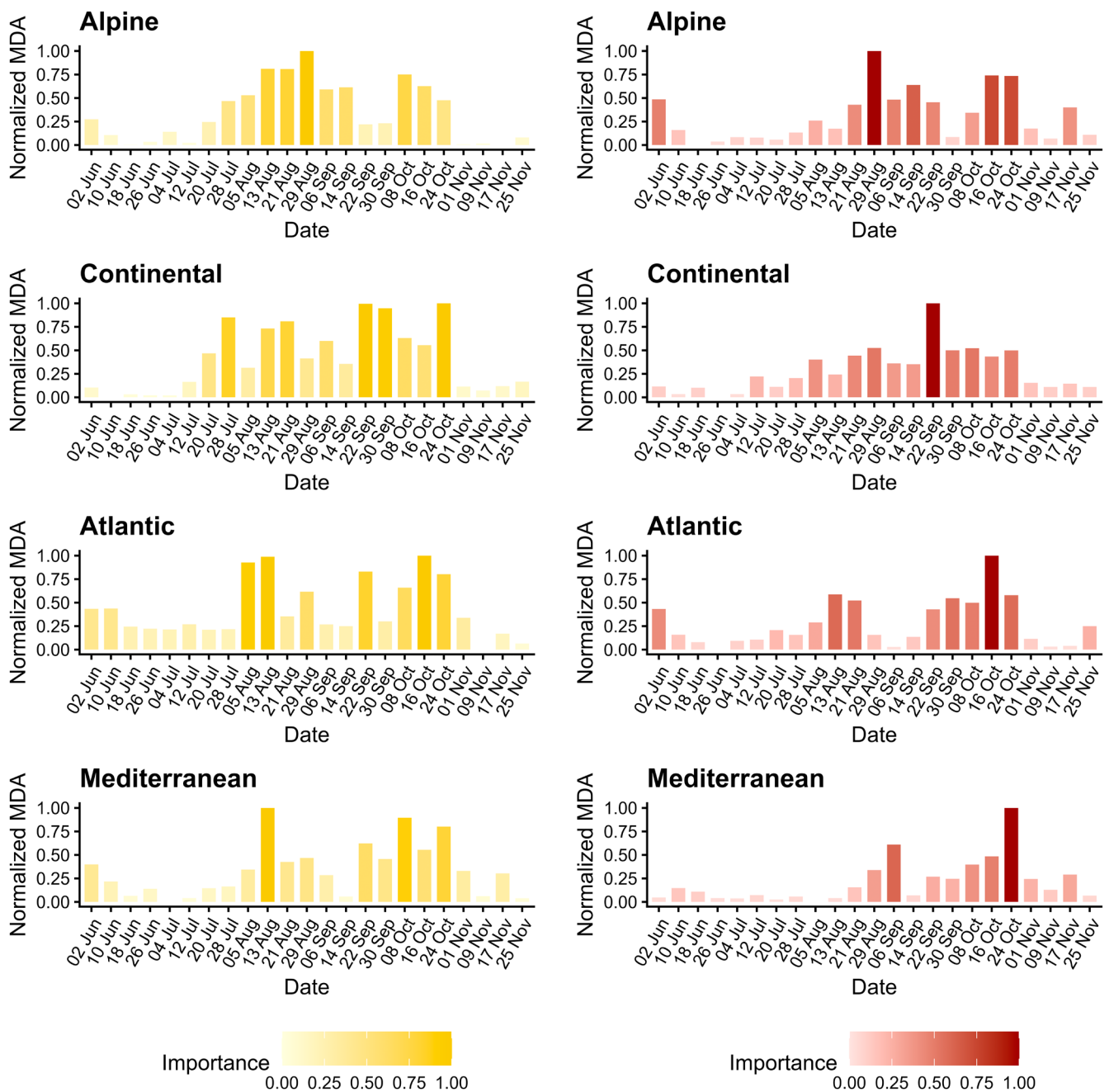


FIGURE 9 | Importance ranking of EVI temporal bands in discriminating dHW-affected profiles, based on mean decrease in accuracy from RF models. Panels show results for moderate (left) and strong (right) dHW intensity across Alpine, Atlantic, Continental, and Mediterranean regions.

productivity under normal conditions but amplifying water demand during heatwave events. When atmospheric dryness peaks, this transpiration cooling capacity is overwhelmed, leaves tend to overheat, and the canopy activity decline scales, (Marchin et al. 2022; Grossiord et al. 2020; Fu et al. 2022), a response that intensifies with heatwave severity. Notably, in the Continental region, the rate of EVI decline appears to slow down under stronger events, potentially indicating a saturating rather than purely linear response. Conversely, the Alpine region showed the most buffered response. In this region, where BDFs are found predominantly in mountainous areas (Antonucci et al. 2021), the reduction in EVI integrals is less pronounced, suggesting a twofold resilience of the population at their marginal distribution influenced by regional

climate specificity and high phenotypic plasticity (Campioli et al. 2024; Petrik et al. 2022). First, an environmental buffer: the prevalence of moderate intensity dHWs and the cooler baseline temperatures provide a first layer of mitigation. Here, microclimatic refugia may act as a protective mechanism (De Lombaerde et al. 2022) as microclimates can be significantly decoupled from macroclimatic temperatures in complex terrain. Second, a phenological buffer: a later growing season peak means the canopy is likely less fully developed and more succulent during the mid-summer dHW peak, potentially making it more resilient than a mature, pre-senescent canopy (Lukasová et al. 2019, 2020). At high altitudes, the delayed growing season implies that Alpine beech forests accumulate less heat exposure and transpiration demand during

peak heat stress months, limiting soil moisture depletion and hydraulic stress (Hua et al. 2022; De Lombaerde et al. 2022). High-altitude populations also show greater phenotypic plasticity in stomatal and leaf traits (Petrik et al. 2022), enabling dynamic adjustments in water-use strategy that may confer additional resilience to episodic heat stress. In contrast, the Mediterranean region exhibited a threshold-type response, where moderate dHWs induced a maximum reduction in productivity, beyond which no further variation was observed. This suggests that even moderate dHW events may push canopy functioning close to physiological limits, so that additional increase in dHW intensity cannot further impact (Loizidou et al. 2016; Martinez del Castillo et al. 2022). This aligns with field evidence of nonlinear stress thresholds under hot-dry Mediterranean summers (Trifković et al. 2022) and likely reflects adaptive mechanisms of southern-edge populations routinely exposed to summer heat constraints (Knutzen et al. 2025; Petrik et al. 2022; Tognetti et al. 2019). Beech populations from drier, warmer sites have evolved to close their stomata earlier under water stress, which reduces water loss but also limits their ability to cool leaves through transpiration (Leuschner 2020; Marchin et al. 2022; Zeppan et al. 2026). In Mediterranean forests, trees enter summer already water-stressed, so even moderate heatwaves push leaf temperatures beyond the damage threshold, triggering stress responses that accelerate leaf degradation and early senescence regardless of heatwave intensity (Marchin et al. 2022; Nguyen et al. 2017; Knutzen et al. 2025), with consequences for within-season productivity and carbon uptake (Frank et al. 2015; Teskey et al. 2015).

4.2 | Lagged Effects of Disruptive Heatwaves

The lagged effect analysis indicates that disruptive heatwaves not only reduce canopy greenness (EVI integrals) but also shift the timing of senescence, highlighting the cascading influence of dHWs beyond the stress period itself, with region-specific patterns. These two levels of response are not independent: the two-stage impact pathway identified in this study reflects the physiological continuum between within-season cellular damage and the downstream triggering of the leaf senescence program. The magnitude and form of the SI decline therefore partially predict the severity and character of the SD advance, as regions experiencing greater within-season canopy impairment are also those where autumn senescence timing is most substantially advanced. In line with the work of Frei et al. (2022) and Descals et al. (2023), our results showed that disruptive heatwaves lead to earlier senescence across all regions, further reducing the annual carbon uptake capacity of these forests and potentially impacting their vitality in current (Pollastrini et al. 2019) and subsequent years (Frei et al. 2022; Schuldts et al. 2020). This legacy effect may be related to different response mechanisms. It may reflect the direct consequence of damage to leaf tissues, inducing diffuse desiccation (Mariën et al. 2021) and premature onset of the leaf coloring phases (Margalef-Marrase et al. 2020). Alternatively, it may result from a mechanism by which trees shorten the transpiration period, thus avoiding extreme dehydration and allowing carbon and nitrogen remobilization through early yellowing (Massonnet

et al. 2021). Early senescence onset has also been reported as a consequence of cumulative physiological response to prolonged heat exposure, accelerating the achievement of seasonal productivity (Zani et al. 2020). Overall, the magnitude of dHW-induced declines in canopy functioning is reflected in the phenological timing of senescence, although the nature of the relationship varies across biogeographical regions.

In the Mediterranean, the advancement of senescence was evident under both moderate and strong dHWs, yet the lack of difference between them mirrors the absence of graded responses. This confirms the hypothesis of a threshold-type behavior as an adaptation mechanism in southern-edge populations. Under already limiting summer conditions, any additional heat stress leaves them with low resilience (Loizidou et al. 2016; Martinez del Castillo et al. 2022) and is sufficient to push them over a pre-existing threshold, initiating a conserved and rapid senescence program regardless of the dHW intensity (Cremonese et al. 2017; Lukasová et al. 2020; Zhou et al. 2025). In the Atlantic, Continental and Alpine regions, moderate and strong dHWs gradually advanced the end of the growing season, consistent with the observed decline in summer canopy activity. In the Alpine region, the dHW impacts described a gradual, linear response, with a minimum senescence advance, hypothetically buffered by a cooler baseline climate and delayed phenology, which translates into a shorter exposure window to heat stress. Similarly, the Atlantic region showed a graded response, but steeper in comparison to the Alpine forests. Here, senescence advanced by up to 13 days under strong dHWs, implying a substantial reduction in the effective growing season. This behavior has important ecological implications, as it limits resource accumulation and alters carbon-water balances at the ecosystem scale (Garonna et al. 2014; Wu et al. 2013). Notably, in the Atlantic region, only strong dHWs produced significant shifts in senescence (in line with the stronger decline in EVI detected under severe stress), implying that vegetation in this temperate, typically well-watered region can buffer moderate heat stress. However, beyond a critical, high-intensity threshold, physiological damage accumulates exponentially and irreversibly, forcing an even earlier senescence. In line with the summer integral analysis, the interpretation of the phenological response in the Continental region requires further investigation, as the patterns observed do not consistently reflect a single type of response, suggesting a more complex behavior. Although both short-term and lagged effects suggest a graded impact with increasing dHW intensity, the rate of change appears to slow down under stronger events, similarly to the Mediterranean response patterns, suggesting the early emergence of adaptation mechanisms even in Continental areas.

4.3 | Biogeographical Gradient of Response and Vulnerability

The Random Forest (RF) analysis provided key insights into the timing of dHW impacts. The consistent identification of two distinct peaks of importance, one in late summer (mid-August to early September) and another in autumn (late September to October), confirmed the complex, multi-stage physiological response to heat stress previously described.

Regional differences mirrored the local growth rhythms. Alpine and Continental sites showed their strongest response in late August–September, reflecting a concentrated sensitivity and an immediate impact on canopy functioning toward the end of the growing season (late summer). In these climates, the growing season is shorter and more temperature-limited (Bajocco et al. 2025), so summer disruptive heatwaves impose an immediate constraint on late-season productivity, amplifying vulnerability. In contrast, Atlantic and Mediterranean sites displayed later peaks, with maximum separability occurring in October and even early November in the Mediterranean region. In these regions, the longer season and recurrent summer water stress mean that heatwave effects may accumulate, and trees can buffer short-term anomalies, but at the cost of a stronger legacy effect later in the season, when carbon and water trade-offs are already critical (Galiano et al. 2011; Lan et al. 2021; Reichstein et al. 2013). In particular, the Mediterranean peak in early November suggests that the most pronounced distinction between affected and unaffected sites emerges during the closing phase of the growing cycle, when water and heat stress interact with the end of the photosynthetic activity period (Zscheischler et al. 2018).

A key finding of this study is that the diagnostic importance of these two phenological phases shifts with the severity of the disruptive heatwave impact. This suggests the existence of a stress-response boundary, which, when crossed, alters the dominant observable symptom of damage. For example, in the Mediterranean region, for moderately affected sites, both the immediate summer EVI decline and the autumn senescence advance are equally important. However, for strongly affected sites, the most critical predictor shifted decisively to the premature senescence signal in late October. This suggests that moderate stress leads to a recoverable, within-season decline in canopy greenness, whereas severe stress triggers delayed impacts that force a markedly earlier termination of the growing season (Descals et al. 2023). Conversely, in the Alpine region, increasing stress severity amplified the importance of the immediate summer impact to the point of near-total dominance. This may reflect the compressed nature of the high-elevation growing season (Bajocco et al. 2025; Hua et al. 2022; Sun et al. 2025), where a vegetative failure during the short peak productivity window leaves little physiological capacity for a delayed senescence phase (Marcis et al. 2025). The legacy is, in effect, consumed by the magnitude of the initial event.

4.4 | Methodological Strengths and Limitations

A key strength of this study is the use of a shifting 30-year baseline for heatwave detection, which effectively accounts for the ongoing warming trend and allows for a more accurate identification of anomalous events relative to the “new normal” climate. A fixed historical baseline risks underestimating the increasing frequency of modern heatwaves; therefore, a moving window is essential for accurate detection (Rosselló et al. 2023). The application of a two-dimensional kernel density estimation (KDE) for detecting phenological anomalies is another robust feature, as it adapts to site-specific conditions and natural interannual variability. This approach aligns with the methodology of Decuyper et al. (2022), who successfully

used a similar kernel density estimation technique to attribute cryptic forest dieback to specific climatic events across Europe. Finally, the success of the Random Forest algorithm in this context highlights the power of machine learning to deconstruct complex, non-linear ecological responses from dense time-series data (Breiman 2001). However, the study is not without limitations. While satellite-based indices like EVI provide consistent, large-scale monitoring, they may integrate multiple stress signals and require careful interpretation in heterogeneous forest canopies (Zeng et al. 2020). The reliance on satellite-derived EVI at a 250 m resolution provides a canopy-level view but cannot capture finer-scale physiological processes or differentiate responses in the understory (Puletti et al. 2018; Ferrara et al. 2023).

Furthermore, although the study links phenological anomalies to preceding heatwaves, it is difficult to fully disentangle the effects of extreme heat from those of drought. Though heat tolerance is correlated with drought tolerance, Hauck et al. (2025) showed that these factors should be regarded as independent when assessing the climate change sensitivity of tree species. The compounding nature of heatwaves and drought, often co-occurring during summer, intensifies physiological stress (Zscheischler et al. 2018). Under such compound conditions, the observed EVI decline and senescence advancement cannot be unambiguously attributed to the thermal component alone, highlighting the need to interpret extreme heat effects within a broader hydroclimatic context.

A related consideration concerns the role of baseline climate conditions. The regional differences in phenological sensitivity may partly reflect differences in the pre-event physiological state of BDF populations. Consequently, the same dHW intensity value may not imply equivalent physiological exposure across and within regions (Cavin and Jump 2017; Leuschner 2020). Furthermore, the identified effects may integrate the cumulative physiological legacy of antecedent conditions, including pre-season frosts, prior-year productivity, and spring phenological timing, that independently modulate canopy vulnerability to subsequent thermal perturbation (Mariën et al. 2021; Wu et al. 2022). Disentangling region-specific physiological sensitivity from region-specific baseline stress state would require pre-event stress indicators currently unavailable at continental scale.

Finally, the 9 km resolution of the temperature data may also mask important microclimatic variations that could buffer or exacerbate heatwave impacts at the local level. Forest canopies are well-documented thermal buffers, with sub-canopy temperatures frequently decoupled from the macroclimate by several degrees, particularly in topographically complex terrain (Wang et al. 2025). This introduces a systematic uncertainty in the comparison of heat stress impacts across biogeographical regions that could be solved only by operating at finer spatial scales.

Our study on dHW effects at continental scale provides a meaningful first-order signal of thermal stress, in terms of both immediate disruption of canopy functioning and lagged shift in phenological timing. Future studies incorporating further complexity factors, like pre-event stress indicators or hydroclimatic

covariates, would substantially improve the causal attribution of the observed phenological shifts and represent a priority for future mechanistic research.

5 | Conclusion

The results of this study have significant implications for forest management and conservation in the face of climate change. The identification of the Continental and Atlantic regions as particularly vulnerable highlights the need for targeted monitoring and adaptive management strategies in these areas. Rising disruptive heatwave frequency and intensity may result in broad growth decline and mortality, fostering a transition in tree species composition. The adaptive traits of marginal populations could be crucial for the species' survival. However, the Mediterranean saturation effect indicates a precarious balance. While resilient to dHW intensity, these populations may be highly vulnerable to repeated, compound events which could push them past their absolute survival threshold. Future research must consider region-specific, asymmetric responses to extreme events. Alongside, forest management strategies cannot be one-size-fits-all; they must be regionally tailored, focusing on reducing competition for water in vulnerable central zones and protecting the genetic reservoirs of resilience in marginal populations. Furthermore, investigating the role of co-occurring stressors, such as drought or pest outbreaks, along with the interaction with other climatic and environmental factors, is critical for developing more accurate predictive models of forest response. In conclusion, this study underscores the importance of explicitly distinguishing between disruptive and non-disruptive events when assessing heatwave impacts on forest phenology and demonstrates that disruptive summer heatwaves represent a significant driver of canopy functioning decline and phenological change in European beech-dominated forests. By elucidating pronounced regional differences in vulnerability, it contributes to offer important insights into the complex mechanisms through which forest ecosystems respond to a warming climate.

Author Contributions

Lorenzo Cesaretti: methodology, formal analysis, data curation, writing – original draft. **Dino Ienco:** data curation, writing – review and editing. **Sofia Bajocco:** conceptualization, methodology, formal analysis, writing – original draft, writing – review and editing, supervision, funding acquisition. **Carlotta Ferrara:** methodology, writing – review and editing, data curation, funding acquisition. **Piermaria Corona:** writing – review and editing.

Acknowledgments

This work was supported by the National Doctorate in Earth Observation (38th cycle) by Sapienza University of Rome, and by the project SOFIA (“Sistemi Organizzati per la Foresta e l’Innovazione Agro-meteorologica”), funded by the Italian Ministry of Agriculture, Food Sovereignty and Forestry (DM 65638).

Funding

This work was supported by the Italian Ministry of Agriculture, Food Sovereignty and Forestry (DM 65638).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset supporting the findings of this study is publicly available on Zenodo: Cesaretti, L., Ferrara, C., Ienco, D., Corona, P., & Bajocco, S. (2025). Dataset of heatwaves affecting European beech forests (v1.0.0); <https://doi.org/10.5281/zenodo.17098110>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Region-specific generalized additive mixed-model (GAMM) smooths in resilient BDF observations, describing the relationship of standardized heatwave intensity with EVI summer integral (SI) and senescence date (SD) across Alpine, Atlantic, Continental, and Mediterranean regions. Black lines show the estimated smooth partial effect of heatwave intensity on the dependent variables (SI and SD), with grey shading indicating the 95% confidence interval. Rug marks along the x-axis denote the distribution of observations. **Figure S2:** Resilient average EVI temporal profiles across biogeographical regions and their standard deviation (shaded areas). “Unaffected” refers to EVI profiles of beech-dominated

forest observations that have not experienced either HWs or PAs, while “Moderate” and “Strong” indicate the corresponding intensity level of heatwaves in profiles that have experienced only HW, without PA. **Figure S3:** Percentage of mean EVI summer integral (SI) decline (top) and senescence date (SD) advance (bottom) according to non-disruptive HW occurrence and intensity in resilient observations, across the four biogeographical regions. **Figure S4:** Summer integral (SI) and senescence date (SD) distribution across biogeographical regions for unaffected (green boxes) and resilient profiles (yellow boxes for moderate, red boxes for strong). Significant differences between categories are reported as follows: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, $****p < 0.0001$, ns = non-significant. Boxes represent the interquartile range (i.e., the 1st and 3rd quartiles), and whiskers extend to 1.5 times the interquartile range. The horizontal line and the cross symbol inside each box represent the median and the mean, respectively. Outliers are shown with an individual dash. **Figure S5:** Importance ranking of EVI temporal bands in discriminating HW-resilient profiles, based on mean decrease in accuracy from RF models. Panels show results for moderate (left) and strong (right) HW intensity across Alpine, Atlantic, Continental, and Mediterranean regions.